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Letter to the Editor

On interpreting responses to low contrast stimuli in terms of magnocellular activity – A few remarks

Lalor and Foxe (2009) used a novel form of Visually Evoked Potentials (VESPA) to study responses to stimuli at different luminance contrasts. In particular, they identified certain responses which they suggest are consistent with activity in the magnocellular system. Lalor and Foxe (2009) raise questions themselves over the validity of their work, such as the use of linear analysis to isolate a part of the visual system that, as they note, is highly nonlinear. While we welcome the possibility of a new means to investigate magnocellular activity, further concerns exist that merit discussion.

First, Lalor and Foxe (2009, p. 127) write: "M [i.e. magnocellular] cells favor ... stimuli with low spatial frequency and high temporal frequency, whereas P cells ... respond best to high spatial frequency and somewhat lower temporal frequency stimuli." However, with regard to spatial frequency, when eccentricity is taken account of, magno- and parvocellular neurons do not actually differ much. Indeed, it has been found that the relationship between spatial resolution and eccentricity in the two cell types is nearly identical (Blakemore & Vital-Durand, 1986, see their Fig. 6; and also Skottun & Skoyles, 2008c). This similarity does not preclude that differences can exist between magno- and parvocellular cells with regard to average spatial frequency tuning or average spatial resolution. For instance, it is possible that the receptive fields of magnocellular neurons are more eccentrically located – in which case they might have a lower average spatial resolution. Rather, the concern is that it is difficult to rely upon such differences in spatial resolution to differentiate magno- from parvocellular neurons when using stimuli confined to any one given eccentricity, or stimuli limited to a narrow range of eccentricities. A consequence of this is that to focus on differences in average spatial tuning properties between magno- and parvocellular cells may not be that relevant and may, in fact, be potentially misleading.

Further, with regard to temporal frequency the difference between magno- and parvocellular neurons would appear to be rather small. For instance, Hawken, Shapley, and Grosof (1996) found no difference in temporal frequency tuning between the two cell types, and Levitt, Schumer, Sherman, Spear, and Movshon (2001) found small differences with regard to averages, and considerable overlap between their distributions. To differentiate magno- and parvocellular neurons on the basis of temporal frequency may therefore be difficult (Skottun & Skoyles, 2008b).

These considerations of spatial and temporal frequency, it should be noted, apply only to stimuli at suprathreshold contrasts. No conflict exists in this regard between the empirical observation that magno- and parvocellular neurons show similar spatial and temporal tuning to suprathreshold stimuli, and the finding – established through lesion studies and human psychophysics (see below) – that the two systems mediate contrast detection at different spatial and temporal frequencies. Moreover, it should be kept in mind that contrast sensitivity and spatial and temporal frequency tuning are two fundamentally different measures: the former is a measure of the lowest detectable contrast, while the latter is a measure of response as a function of spatial or temporal frequency (for a fixed suprathreshold contrast). As a result, it is necessary to make a clear distinction between the use of stimuli at or near contrast threshold and that of suprathreshold stimuli like those used to elicit VEPs. Thus, even though the magnocellular system mediates contrast detection at low spatial frequencies, it should not be assumed that this system will also substantially favor stimuli with low spatial frequencies at suprathreshold contrasts.

Second, Lalor and Foxe (2009) interpret the responses obtained with low contrast stimuli in terms of magnocellular activity. There are reasons for caution in this regard since there exists evidence to indicate that under many stimulus conditions the parvocellular system responds to lower contrast than the magnocellular system. The alternative idea that the magnocellular system responds to lower contrast than the parvocellular system stems mainly from single cell recordings (e.g. Kaplan, 1991; Kaplan & Shapley, 1986). However, behavioral studies of contrast sensitivity in monkeys following magno- and parvocellular lesions are at conflict with the single cell research since they reveal that the largest reductions in contrast sensitivity occur following parvocellular lesions (Merigan, Byrne, & Maunsell, 1991; Merigan, Katz, & Maunsell, 1991; Merigan & Maunsell, 1990, 1993; Schiller, Logothetis, & Charles, 1990a, 1990b). The results from lesion studies are also consistent with human psychophysics (e.g. Kulikowski & Tolhurst, 1973; Legge, 1978; Tolhurst, 1975). Together these observations suggest that when a behavioral test is used, it is the parvocellular system which, under most conditions, will show responses to the lower contrast. The magnocellular system has lower contrast threshold only when the stimuli are of low spatial frequency and/or high temporal frequency. (It is this fact which makes contrast sensitivity such a reliable test of magnocellular, and parvocellular, sensitivities, Skottun, 2000.) Given the discrepancy between single cell recordings and behavioral studies some caution is therefore needed with regard to attributing VEP responses elicited with low contrast stimuli to the magnocellular system. This is particularly the case when using stimuli with broad spatial and temporal frequency spectra such as the ones used by Lalor and Foxe (2009).

The third point is with regard to the higher contrast gain at low contrast in magnocellular neurons than in parvocellular cells. Lalor and Foxe (2009) provide this difference in gain as the reason for attributing responses to low contrast stimuli to the magnocellular system. Although evidence indicates that magno- and parvocellular neurons differ with regard to contrast gain (Kaplan & Shapley, 1986), other neurons exist which show contrast-response characteristics similar to those of magno- and parvocellular neurons. Thus, one might be able to use contrast gain to isolate magnocellular responses – or to bias stimulation for this system – if one

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could reasonably assume that the magno- and parvocellular systems were the only ones involved. However, contributions from other structures cannot be excluded particularly when recording is made from the scalp above the visual cortex. For instance, there exist koniocellular inputs to the visual cortex. Koniocellular neurons, moreover, at least in owl monkeys (*Aotus Azarae*), have been found to have saturation characteristics similar to those of magnocellular neurons (Kilavik, Silveira, & Kremers, 2007). Also, neurons in the Middle Temporal Area (Area MT) show high contrast gain and saturation that is similar to those of magnocellular neurons (Sclar, Maunsell, & Lennie, 1990). A low degree of saturation, similar to that of parvocellular neurons, on the other hand, can be observed in the primary visual cortex, i.e. in V1 (Sclar et al., 1990). Thus, it seems difficult to differentiate, on the basis of contrast gain and saturation, contributions that are uniquely magno- and parvocellular from cortical activity.

Given that Area MT is part of the dorsal cortical stream, it is relevant, that the technique used by Lalor and Foxe (2009, p. 128), according to these authors, "may favor midline structures ... and perhaps also regions in the dorsal visual stream." Since Area MT receives koniocellular inputs (Sincich, Park, Wohlgemuth, & Horton, 2004) as well as inputs of parvocellular origin (Merigan & Maunsell, 1993; Nassi, Lyon, & Callaway, 2006) (in addition to inputs of magnocellular origin), it is, as a result, far from certain, that signals from Area MT will reflect only magnocellular activity.

One potential application of the method of Lalor and Foxe (2009) would be to investigate clinical conditions under which the magnocellular pathway might be impaired. In this connection, it is worth noting that Lalor and Foxe (2009, p.127) write that "M [i.e. magnocellular] pathway function has been reported to be relatively more impaired in ... schizophrenia ... and dyslexia." However, reviews of contrast sensitivity studies find little support for linking either of these two conditions specifically to magnocellular dysfunction (Skottun, 2000; Skottun & Skoyles, 2007, 2008a). In the case of schizophrenia, visual masking fails also to provide substantial support for a magnocellular deficit (Skottun & Skoyles, 2009).

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